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Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana

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Water depth requirements, diet, feeding styles and diurnal activity patterns are described for waterbirds using two brackish water lagoon systems in coastal Ghana, the Songor and Keta Lagoons. We project the habitat and activity data on a guild structure defined on the basis of individual feeding style and the sensory mechanism used to detect food. A total of 3199 flocks containing 118,648 individuals of 36 different waterbird species were examined during October–November 1994. Feeding habitats varied from dry mudflats to wet mud and shallow water of not more than 20 cm. The depth of water selected by waterbirds for foraging (but not for roosting) was correlated with tarsus length. Foraging birds exhibited a wide range of feeding styles using visual and/or tactile means for detecting prey: pecking, probing, stabbing, sweeping and ploughing, sometimes feeding singly, communally or socially in loose or dense flocks. Prey items taken ranged from seeds of Widgeongrass *Ruppia maritima* to invertebrates (mainly polychaetes, molluscs and crabs) and fish, mainly juvenile Tilapia. The daytime was spent on two main activities, feeding and roosting, with a small fraction of the time (average of 10% for 25 species) spent on comfort activities. The waterbirds exhibited either a circadian (most waders, except Common Sandpipers *Actitis hypoleucos* and Turnstones *Arenaria interpres*) or a diurnal foraging activity pattern (herons and terns), with no purely nocturnal species. Some species fed throughout the day, others showed peak foraging at various times of the day. The proportion of time spent foraging was related to guild (highest in visual and tactile surface-foraging waders) and was negatively correlated with the size of the species. We conclude that the observed patterns in the use of the 24-h day by waterbirds for foraging are not species specific but vary depending on conditions on the feeding grounds. Nocturnal foraging is a normal and a regular strategy used by waterbirds to obtain enough food to fulfill their energetic requirements, so that irrespective of the sensory mechanism used to detect prey and the conditions prevailing on the feeding grounds, waterbirds forage day and night as dictated by their energetic needs. Water depth appears to be the key environmental factor controlling the availability of food for the waterbirds in the Ghanaian lagoons.

The coastal wetlands of Ghana are known to support internationally important numbers of migratory waterbirds (Grimes 1969, Ntiamoa-Baidu & Grieve 1987, Ntiamoa-Baidu 1991, Ntiamoa-Baidu & Hollis 1992, Piersma & Ntiamoa-Baidu 1995, Van Gaalen & Van Gelderen 1995). The value of the wetlands as staging areas and wintering grounds has also been established through long-term monitoring of waterbird numbers (initiated under the Save the Seashore Birds Project–Ghana and run since 1986) and ringing studies (Ntiamoa-Baidu & Hepburn 1988, Ntiamoa-Baidu 1991, 1993). Migrant waterbirds begin to arrive on

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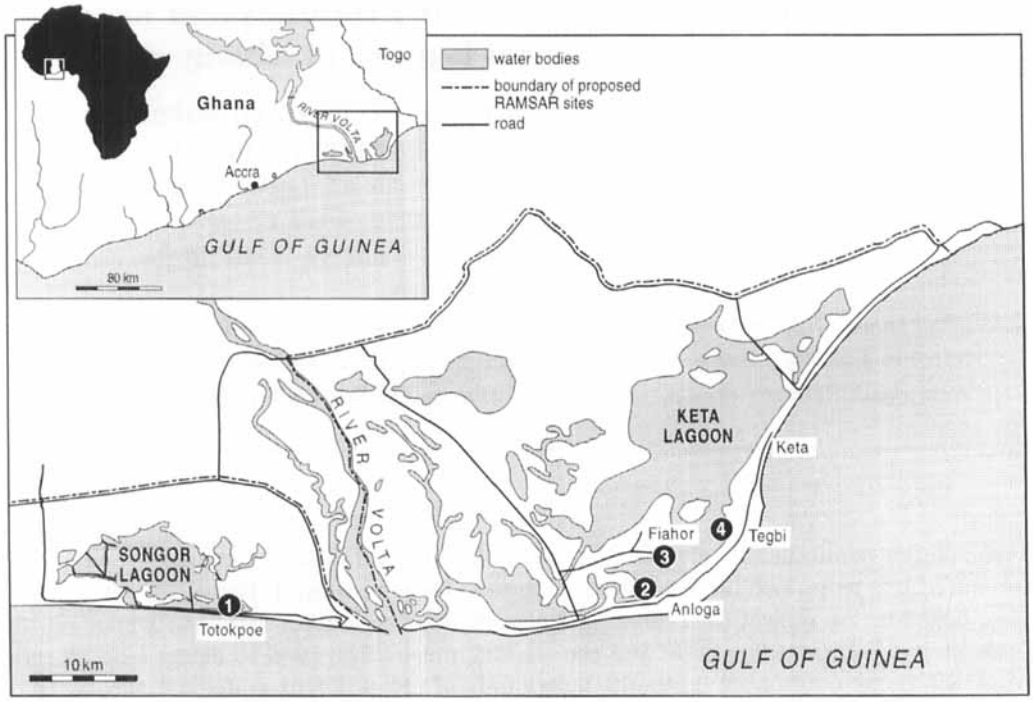

Figure 1. Map of eastern Ghana coast showing the two lagoon systems west and east of the Volta River mouth, Songor Lagoon and Keta Lagoon. The research sites at Totokpoe (1) (Songor), Anloga (2), Fiahor (3) and Tegbi (4) (all Keta) are indicated with circled numbers.

the Ghanaian coast from the end of August–early September and remain until April, with the highest numbers occurring from September to December. Waterbirds are thus most abundant on the Ghanaian coast during the dry season when water levels in the lagoons are falling and the shallow waters and exposed mud flats offer favourable conditions for foraging. Despite the well documented ornithological importance of the Ghanaian coastal wetlands, the roles of individual bird species in the wetland ecosystem and the factors which influence the use of the wetlands by the birds have not been studied.

The key factors which influence habitat selection by migrant waterbirds during the nonbreeding season are availability of food, safe roosting sites and the extent of disturbance (Hochbaum 1955, Myers 1984, Van Eerden 1984, Ens *et al.* 1990, 1994, Piersma 1994). On the feeding grounds, waterbird distribution is largely determined by distribution of food, the substrate type and the distance from feeding area to roosting site in species which utilize different sites for feeding and roosting (Zwarts 1974). Foraging behaviour and daily activity patterns have been studied for several waterbird species, initially mostly concentrated in temperate areas (Goss-Custard 1969, Heppleston 1971, Goss-Custard *et al.* 1977, Pienkowski 1981, 1982, Ketzenberg & Exo 1994) and more recently in a few tropical areas (Robert & McNeil 1989, Robert *et al.* 1989, Morrier & McNeil 1991, Kalejta 1992). Factors which have been reported to influence foraging behaviour include seasonal effects (Goss-Custard *et al.* 1977, Zwarts *et al.* 1990, Piersma *et al.* 1994), tidal effects (Burger *et al.* 1977, Connors *et al.* 1981, Engelmoer 1982, Burger 1984, Piersma *et al.* 1993, Hötker 1995) and human disturbance (Burger & Gochfeld 1991, Koolhaas *et al.* 1993). Most of these studies considered single species or a small number of species in intertidal habitats. Fasola and Canova's (1993) study at Lake Turkana, Kenya, was the first attempt to describe the activity rhythm and time budgets of a waterbird community using a standing water ecosystem in tropical Africa.

This study describes the water depth requirements, diet, feeding styles and diurnal activity patterns of 36 of the more than 50 species of waterbirds that inhabit two brackish water lagoon systems in coastal Ghana, Songor and Keta Lagoons (Fig. 1). The goal of the study was to provide data both for the understanding of the ecological characteristics and requirements of waterbirds using poorly known African wetland habitats and for comparative studies of the biology of these lesser known waterbird species. We believe that the detailed quantification of the ecological requirements of waterbird species, linked with appropriate descriptions of relevant ecological parameters, can be used profitably for large-scale assessments and monitoring of the ecological value of the wetlands to guide conservation and management activities.

DEFINING THE GUILDS

The Volta lagoons were inhabited by almost 50 waterbird species in October–November 1994 (Piersma & Ntiamoa-

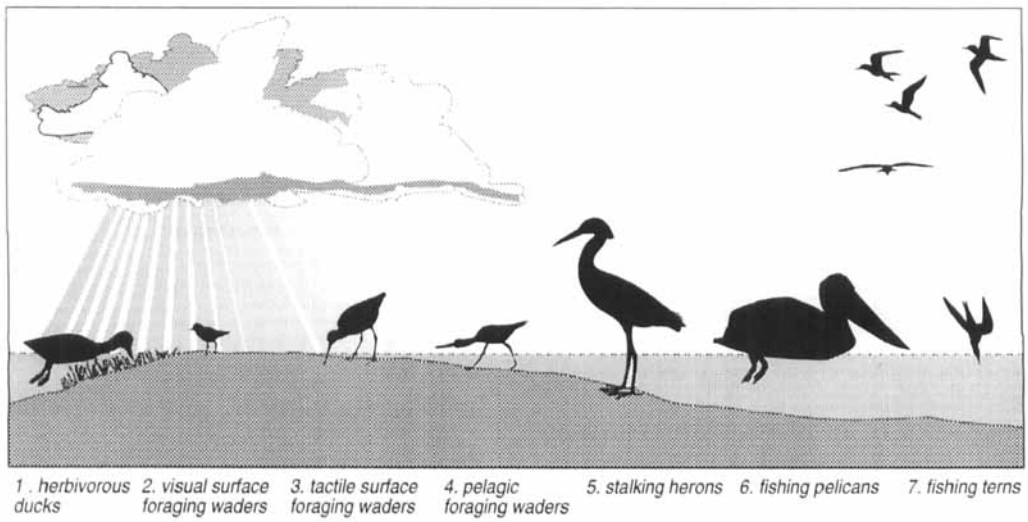

Figure 2. Pictorial representation of the seven waterbird guilds using the coastal lagoons of Ghana. See text for explanations.

Baidu 1995). Thirty-six of these were observed in sufficient numbers and frequently enough during the study period to allow brief descriptions of their ecology; but even 36 species are too many to discuss easily in ecological terms. We therefore use the concept of "guild" to structure our information on waterbirds' foraging habits, diurnal rhythms and diets. Root (1967) introduced the concept of functional species groups or guilds, indicating species assemblies that exploit the same class of resources in a similar way. Guilds can be defined *a posteriori* (subjective or more objective) on the basis of clustering, with reference to foraging habits, habitat choice and diets (Holmes & Recher 1986). Guild can also be derived *a priori* on the basis of morphological characters (Ricklefs & Travis 1980). We have defined guilds subjectively on the basis of literature information on the sensory mechanism used to detect food (a major determinant of the feeding niche; Piersma 1996a,b) and field observations of feeding style (Myers 1984). Information on diet, diurnal habits and habitat characteristics were projected on this guild structure to describe the ecological characteristics of the waterbird community in Ghana's coastal lagoons.

Our structuring of the waterbird community yielded seven guilds (Fig. 2), four of which consist of tight taxonomic groupings: the herbivorous tree ducks (guild 1), the (stalking) herons (guild 5), the (fishing) pelicans (guild 6) and the (fishing) terns (guild 7). Although herons, pelicans and terns all feed on fish, they obtain their prey in very different ways. The remaining species are all ground-feeding waders, which were split up into three guilds: two groups of surface foragers, one of which predominantly uses visual means to detect the prey (guild 2) and another which predominantly uses tactile means to find prey (guild 3), and the third (guild 4), comprised of pelagic foragers (tringid sandpipers and stiltlike birds) which fish in the water layer and use visual as well as tactile senses to detect prey. In summary, the seven guilds are

(1) Herbivorous ducks (comprising the Fulvous Tree Duck *Dendrocygna bicolor* and the White-faced Tree Duck *Dendrocygna viduata*).

(2) Visual surface-foraging waders (comprising Kittlitz's Plover *Charadrius pecuarius*, White-fronted Plover *Charadrius marginatus*, Ringed Plover *Charadrius hiaticula*, Grey Plover *Pluvialis squatarola*, Common Sandpiper *Actitis hypoleucos*, Whimbrel *Limosa phaeopus*, Turnstone *Arenaria interpres*, Wood Sandpiper *Tringa glareola* and Redshank *Tringa totanus*).

(3) Tactile surface-foraging waders (comprising Black-tailed Godwit *Limosa limosa*, Bar-tailed Godwit *Limosa lapponica*, Curlew *Numenius arquata*, Knot *Calidris canutus*, Sanderling *Calidris alba*, Little Stint *Calidris minuta* and Curlew Sandpiper *Calidris ferruginea*).

(4) Pelagic-foraging waders (comprising Marsh Sandpiper *Tringa stagnatilis*, Greenshank *Tringa nebularia*, Spotted Redshank *Tringa erythropus*, Black-winged Stilt *Himantopus himantopus* and Avocet *Recurvirostra avosetta*).

(5) Stalking herons (comprising Little Egret *Egretta garzetta garzetta*, Reef Heron *Egretta garzetta gularis*, Great White Egret *Egretta alba* and Grey Heron *Ardea cinerea*).

(6) Fishing pelicans (comprising the White Pelican *Pelecanus onocrotalus* and Pink-backed Pelican *Pelecanus rufescens*, a single record).

(7) Fishing terns (comprising Little Tern *Sterna albifrons*, Common Tern *Sterna hirundo*, Roseate Tern *Sterna dougallii*, Sandwich Tern *Sterna sandvicensis*, Royal Tern *Sterna maxima*, Caspian Tern *Sterna caspia*, Whiskered Tern *Chlidonias hybridus* and Black Tern *Chlidonias niger*).

STUDY AREAS

The study sites comprised the two lagoons associated with the River Volta delta in Ghana: Songor Lagoon (west of the

Volta estuary, 05°49'N, 00°28'E) and Keta Lagoon (east of the Volta estuary, 05°55'N, 00°59'E; Fig. 1). Together, the two sites form the largest and most important wetland for waterbirds along the Ghana coast (Ntiamoa-Baidu & Hepburn 1988, Ntiamoa-Baidu 1991, 1993). Both lagoon systems comprise shallow brackish water bodies with extensive mudflats and islands. The open water of Songor covers *c.* 115 km^2 and extends *c.* 20 km along the coast and *c.* 8 km inland behind a narrow sand dune on which a number of villages are situated. Keta Lagoon covers roughly 300 km^2 and stretches for 40 km along the coast. Keta Lagoon is separated from the sea by a narrow coastal ridge which is 2.5 km at its widest point and less than 1 km at its narrowest portion.

With the construction of the Akosombo dam and regulation of the flow from the Volta River in 1964, inflow into both lagoons from the Volta River was reduced. Songor receives freshwater inflow from a number of small streams including the Sege, while Keta collects water from the Todzie, Aka and Belikpa Rivers. The main freshwater inputs to the lagoons are direct rainfall and surface runoff. During the rainy season, the water levels rise rapidly and often overflow the banks, resulting in inundation of surrounding lands. In the dry season (November–March), large sections of both lagoons dry up, leaving pools of hypersaline water. Songor Lagoon has no direct access to the sea, and saline water is replenished by seepage through the sand dunes. Keta Lagoon is reported to be an open lagoon (Kwei 1977, Mensah 1979), but it was effectively closed in October–November 1994 when the study was carried out. Large areas of both Songor and Keta had already dried up in October 1994, and the wader feeding studies concentrated on four sections (Fig. 1B), Totokpoe (Songor Lagoon) and Fiahor, Anloga and Tegbi (Keta Lagoon), which contained water and where the largest concentrations of birds were found (Piersma & Ntiamoa-Baidu 1995). The water depth in all the study areas was less than 40 cm, water temperatures ranged from a minimum of 22°C at night to 34°C in the afternoon and the salinities were high in all areas (40–100 ppt) except an area of seepage water at Totokpoe which was 27 ppt.

At Totokpoe, a continuous seepage of seawater through the dune ridge kept the southern edges of the lagoon wet; such areas were much wetter in the early morning than later in the day because of the high rate of evaporation. The bottom substrate was very soft mud and there was a high coverage of Widgeongrass *Ruppia maritima* in areas with standing water. A small corridor of mangrove trees (*Rhizophora* sp.) bordered the dune ridge in the seepage areas at the western limit of the standing water.

At Fiahor, the main water body south of the village was about 500 m from the normal high water mark and a large, dry mud bank extended eastward approximately 1500 m into the lagoon. A continuous stretch of mudflats extended from Fiahor through Anloga to Tegbi, and although the extent of water coverage in the Keta Lagoon was very low during the study period, the water reached within 200 m of the permanent higher shore at Tegbi. In addition, afternoon breezes pushed the water temporarily over parts of the dry flats. The substrate at the Keta sites was generally firmer and much more sandy than at the Songor site. The vegetation in the areas used by the birds consisted mainly of submerged plant material, dominated by Widgeongrass. An extensive *Typha* marsh occurred along the point of freshwater inflow and the complex network of channels and pools at Anloga.

METHODS

Recording habitats and activity patterns

The study was undertaken in October–November 1994. Reconnaissance visits were undertaken to all the sites for observations on the general terrain and habitat types prior to the intensive field study. The bulk of the data on the time-activity budget of the ground-based waterbirds were collected systematically during 24-h observation programs carried out five times at Keta Lagoon and three all-day observations at Songor (it was not profitable to do night observations at this site). Additional information was collected opportunistically during the numerous visits to the various parts of the two lagoons for general ornithological studies. Observations were made with the use of zoom telescopes (magnification ×15–×60) during daylight and at dusk and dawn and with a Delnocta night scope (magnification ×5) during darkness. A small infrared beam was used to enhance the clarity of the light-intensified image on the night scope. At night, flocks were often too distant for this equipment to yield reliable species identification and foraging observations, and only a few quantitative observations could be collected.

Waterbird flocks were scanned instantaneously, and records were taken of three behavioural categories: (1) feeding, (2) comfort activities (preening, bathing, stretching) and (3) roosting (sleeping, standing). Flocks were considered separate if the distance between the nearest birds was 20 or more bird lengths. Scanning usually demanded rapid assessments on the part of the observers since, especially in foraging flocks, the birds moved rapidly and erratically and the detailed situation was continuously changing every few seconds. For each species in a flock, water depth was estimated from the level of water relative to exposed vertical leg length (in 0.1 intervals on a scale of 0.0–1.0, and 1.0 when birds were standing belly deep in water). These relative leg lengths were converted to depth from scale drawings or from photographs of the birds concerned. Table 1 summarizes the lengths of legs used in this study.

For each bird species, differences between the feeding activities in different periods of the day were tested with an ANOVA after carrying out arcsine-transformation of the foraging percentages. Fisher's least significant difference tests were used for multiple comparisons. All statistics were performed in SYSTAT.

Table 1. *Body mass and leg lengths (as used in this study) of the different waterbird species that foraged upright in shallow water of the Keta and Songor Lagoons*

Species	Body mass (g)	Exposed leg length (mm)
Kittlitz's Plover	30	30
White-fronted Plover	45	31
Ringed Plover	50	35
Grey Plover	250	71
Common Sandpiper	55	31
Whimbrel	300	86
Turnstone	100	34
Wood Sandpiper	60	46
Redshank	105	68
Black-tailed Godwit	210	123
Bar-tailed Godwit	250	84
Curlew	800	111
Knot	120	42
Sanderling	55	33
Little Stint	25	33
Curlew Sandpiper	65	45
Marsh Sandpiper	70	75
Spotted Redshank	140	86
Black-winged Stilt	200	174
Avocet	260	143
Little Egret	500	135
Reef Heron	500	135
Grey Heron	1350	208

Feeding style and diets

Whenever activity and water depth scans were carried out, we also made detailed observations on the style of feeding (how prey items were hunted or searched for and methods used for catching/obtaining the prey) of the different waterbird species comprising the flocks under observation. Prey items and intake rates were also recorded by direct observations using telescopes. Data on prey items obtained through the direct visual observations were further supplemented by collecting and analysing the contents of faecal droppings of birds wherever possible.

RESULTS

A total of 3199 flocks containing 118,648 individuals of 36 different waterbird species were scanned during the study period. Table 2 summarizes all the observations on feeding styles, feeding habitats, diets and feeding rhythms of the waterbird species using Songor and Keta Lagoons.

Water depth selection

Figure 3 shows the ranges of water depth selected by foraging birds belonging to different guilds. Feeding habitats

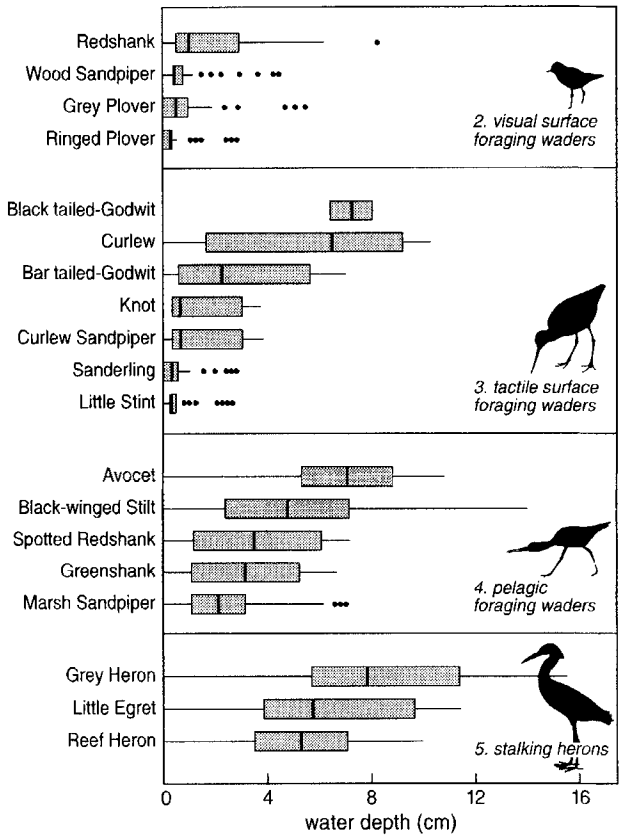

Figure 3. Water depths selected by foraging waterbird species representative of four of the seven waterbird guilds in Songor and Keta Lagoons in October–November 1994. The data are presented as box-plots, giving the median, the two central quartiles and the range (plus outliers indicated with dots) of water depth values estimated from exposed leg length. Sample sizes are presented in Table 3.

varied from dry mudflats to wet mud and shallow water of no more than 20 cm. Small waders, e.g. Ringed Plover, Sanderling and Little Stint, foraged on the dry banks, wet mud and water which was less than 3 cm deep; medium sized waders such as Black-winged Stilt, Greenshank and Bar-tailed Godwit required water depths up to 10 cm for feeding, while the relatively big egrets and herons fed in water up to 17 cm deep. The spatial distribution patterns of feeding waders on the lagoon can be summarized as follows: visual surface foraging waders (guild 2) such as Ringed Plover, Kittlitz's Plover, White-fronted Plover, Little Stint, Turnstone, Grey Plover and Common Sandpiper foraged on the outer edges and wet mudbanks. They were followed by species such as Curlew Sandpiper, Sanderling and Knot (guild 3) and Marsh Sandpiper (guild 4) in the shallow water margins, with Greenshank, Spotted Redshank, Black-winged Stilt (guild 4) in the deeper water and the herons (guild 5) in the inner layer. The choice of feeding habitats depended on food availability because the birds were not observed to feed in areas which were flooded a few days previously and were devoid of prey items. The depth of water selected for

Table 2. *Characteristics of feeding habitat, feeding style and diet of the waterbirds using Songor and Keta Lagoons in October–November 1994*

Species	Feeding style	Guild[a]	Feeding habitat (water depth, cm)	Degree of flocking during foraging	Incidence of social foraging	Diet	Diurnal feeding rhythm
Fulvous Tree Duck	Grazing	1	?	Strong	Always	Weeds, seeds	?
White-faced Tree Duck	Grazing	1	?	Strong	Always	Weeds, seeds	?
Kittlitz's Plover	Pecking	2	0–1	Weak	Never	Invertebrates	24 h
White-fronted Plover	Pecking	2	0–2	Weak	Never	Invertebrates	24 h
Ringed Plover	Pecking	2	0–3	Weak	Never	Invertebrates	24 h
Grey Plover	Pecking	2	0–5	None	Never	Mainly worms	24 h
Common Sandpiper	Pecking	2	0–1	None	Never	Arthropods	Day
Whimbrel	Pecking	2	0	None	Never	Crabs	Day
Turnstone	Pecking	2	0–2	Weak	Never	Invertebrates	Day
Wood Sandpiper	Pecking	2	0–4	Weak	Never	Invertebrates	24 h
Redshank	Pecking	2	0–6	Weak	Sometimes	Invertebrates, fish	24 h
Black-tailed Godwit	Probing	3	5–10	Strong	Never	Molluscs	24 h
Bar-tailed Godwit	Probing	3	0–7	Strong	Never	Worms	24 h
Curlew	Probing	3	0–12	Weak	Never	Crabs, worms	24 h
Knot	Probing	3	0–3	Strong	Never	Molluscs, seeds	24 h
Sanderling	Pecking, probing	3	0–2	Strong	Never	Invertebrates	24 h
Little Stint	Pecking, probing	3	0–2	Strong	Never	Invertebrates	24 h
Curlew Sandpiper	Pecking, probing	3	0–3	Strong	Never	Invertebrates, seeds	24 h
Marsh Sandpiper	Pecking, ploughing	4	1–7	Strong	Often	Fish	24 h
Greenshank	Pecking, ploughing	4	1–7	Strong	Usually	Fish	24 h
Spotted Redshank	Pecking, ploughing	4	1–7	Strong	Usually	Fish	24 h
Black-winged Stilt	Probing, pecking, sweeping	4	0–14	Variable	Sometimes	Fish, invertebrates	24 h
Avocet	Sweeping	4	2–11	Strong	Always	Fish	24 h
Little Egret	Stabbing	5	2–15	Weak	—	Fish	Day
Reef Heron	Stabbing	5	2–15	Weak	—	Fish	Day
Great White Egret	Stabbing	5	2–15	Weak	—	Fish	Day
Grey Heron	Stabbing	5	2–17	Weak	Rarely	Fish	Day
White Pelican	Scooping	6	>30	Strong	Always	Fish	Crepuscular
Little Tern	Diving	7	Lagoon	—	—	Fish	Day
Common Tern	Diving	7	Sea	—	—	Fish	Day
Roseate Tern	Diving	7	Sea	—	—	Fish	Day
Sandwich Tern	Diving	7	Sea	—	—	Fish	Day
Royal Tern	Diving	7	Sea	—	—	Fish	Day
Caspian Tern	Diving	7	Lagoon	—	—	Fish	Day
Whiskered Tern	Diving	7	Lagoon	—	—	Fish	Day
Black Tern	Diving	7	Sea	—	—	Fish	Day

[a] 1, Herbivorous ducks; 2, visual surface-foraging waders; 3, tactile surface-foraging waders; 4, pelagic-foraging waders; 5, herons; 6, pelicans; 7, terns.

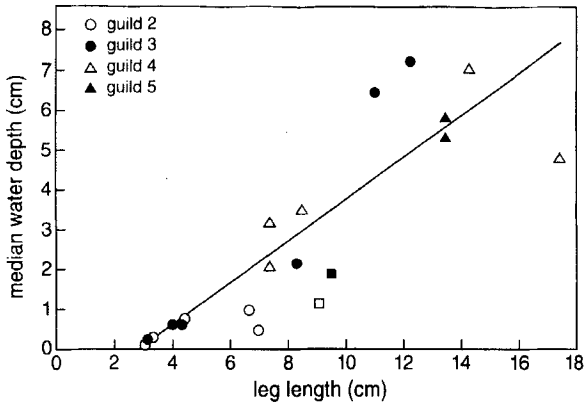

Figure 4. Water depths selected by foraging waterbirds as a function of exposed leg length in the different species. Details of the regression line are given in the text.

foraging was significantly correlated with the tarsus length of the bird ($r^2_{20} = 0.82$, $P < 0.001$; Fig. 4).

Roosting sites comprised dry mud banks, islands within the lagoons and shallow water up to 16 cm deep. Herons and egrets also roosted commonly on structures in the water, such as sticks used by fishermen for constructing fishing devices. There was no significant correlation between water depth and leg length for roosting birds ($r^2_{20} = 0.05$, m.s.) although there was a tendency for bigger birds to select deeper water. All the tern species used the exposed mudbanks of the lagoons as roosting habitat and foraged mainly at sea. Little Terns, Black Terns, Whiskered Terns and Caspian Terns sometimes foraged on the lagoons.

Feeding styles

The waterbirds using the lagoons exhibited a range of feeding patterns. Individuals occasionally fed solitarily, but most of the time the birds fed communally in loose or dense, small or large, mixed species aggregations or socially in small or large flocks. Flock sizes ranged from 2 to 600 birds, with most individual birds feeding in flocks of 50 or larger (Fig. 5). A social foraging flock was defined as a dense flock of waterbirds, members of which were all foraging simultaneously, giving an impression of an organized formation. In a social foraging flock, members of the flock all moved in a synchronised fashion in one direction, thus giving the impression of a single large "organism". The phenomenon was particularly evident in Greenshank, Spotted Redshank, Marsh Sandpiper, Avocet and White Pelican.

Some of the smaller waders would intermittently run, pause and watch, and then take another run, sometimes to catch a surface-living benthic invertebrate or fish, obviously using visual means for detecting the prey items. This mode was predominant among the plovers in guild 2. Other species in the same guild, e.g. Wood Sandpiper and Redshank, also gave the impression of feeding by eyesight but appeared to be pecking randomly on the surface of the water or mud. Some of the waders feeding on exposed mud would walk and frequently probe in the mud, clearly using tactile means to discover buried prey (guild 3). The waders feeding in dense flocks in shallow water fed by moving their slightly opened bills rapidly through the water, basically ploughing through the water (guild 4). In such cases, the bird immersed the lower half of its bill in the water at a shallow angle and ran forward very quickly for a distance of 5–15 m pursuing its fish prey (mainly small Tilapia). Species such as Avocet and Spotted Redshank fed mostly in social foraging flocks and swept or scythed the bill through the water (Pierce 1985) as the main feeding technique. This technique was also used by Greenshanks when they fed in social foraging flocks and was seldom seen in singly foraging birds except for the occasional Black-winged Stilt. Black-winged Stilts exhibited a wide range of feeding styles: pecking, probing, sweeping and ploughing, sometimes feeding singly, in loose flocks or joining in social foraging flocks. Large, stalking waterbirds, like herons (guild 5), walked slowly through shallow water searching for prey items, or stood motionless

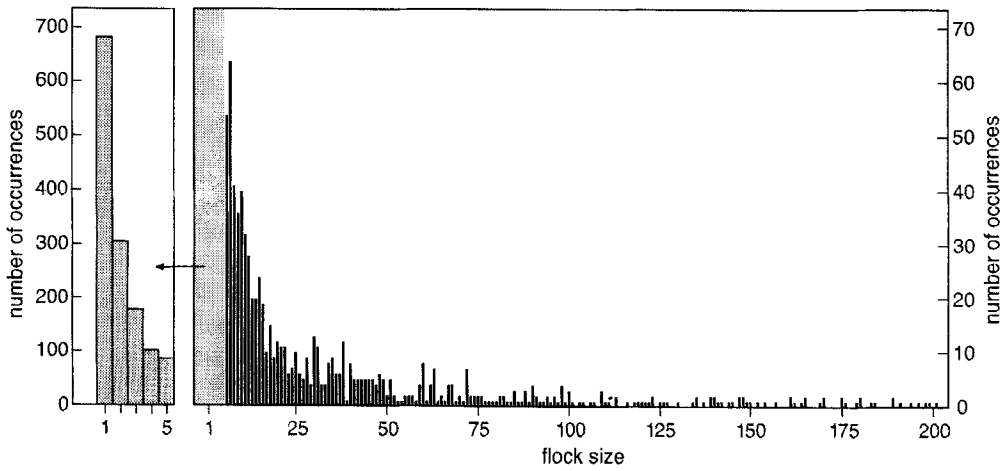

Figure 5. Distribution of flock sizes (all bird species combined) in Songor and Keta Lagoons in October–November 1994.

watching for the prey and stabbing it when found. They would also often join aggregations of communally and frantically feeding waders, thus trying to capitalize on the confusion created by the rapid movements of the waders amongst the fish prey.

Diets

Prey items taken by the different waterbird species (detailed in Table 2) ranged from seeds of Widgeongrass to various invertebrates (mainly polychaetes, molluscs and crabs) and fish. The fish taken by waterbirds were mostly juvenile Tilapia, of which five species occurred: *Saratherodon melanotheron* (numerically dominant), *Oreochromis niloticus, Tilapia zillii, Hemichromis faciatus* and *Hemichromis bimaculatus*. All the species in guilds 2 and 3 (plovers and sandpipers) fed on invertebrates and seeds and either pecked from the surface or probed in the mud for the prey. The shanks, stilts, herons and terns (guilds 4–7), fed mainly on fish.

Diel rhythmicity

Because of the limitations in the night viewing equipment, the records on proportion of time spent on different activities at night were pooled together and presented as whether or not species foraged at night (Table 2). Of the 25 species of waterbirds for which substantial time-activity data were obtained, 18 showed a circadian activity pattern, feeding by day and night, while the remaining seven were diurnal; there were no purely nocturnal species. Waterbirds which fed by day and night comprised the White Pelican, all species in guild 4, all species in guild 3 and six of the eight species in guild 2. Three species in guild 2 (Common Sandpiper, Turnstone and Whimbrel) and all species in guild 5 fed only in daylight. All the seven species of terns present on the lagoons foraged mainly out at sea during the day. Mass departures of terns out to sea from the roosting site on the lagoon were observed just before dawn, whereas numbers returning from the sea to the roost peaked at dusk. However, the movement of terns between the lagoons and the sea continued throughout the day.

Figures 6–9 give the details of the activity patterns of selected species representing the various waterbird guilds. Most wader species showed a decrease in foraging activity at midday, the timing of the minima varying from species to species. Clear exceptions to this general pattern were Grey Plover (with two dips in feeding activity, one in the morning and another in the afternoon; Fig. 6) and the Greenshank and Avocet (Fig. 8), both of which fed little during the daytime periods. In the Little Egret and Reef Heron, but not the Grey Heron (Fig. 9), the percentage roosting increased in the course of the daylight period, with no increase in foraging towards nightfall. To test whether the diurnal variations apparent in Figures 6–9 were statistically different from a random pattern, we carried out a series of ANOVAs (Table 4). Only in Ringed Plover, Sanderling, Little Stint, Curlew Sandpiper and Black-winged Stilt was this difference significant. In each of these species, there was a reduction in foraging activity around midday, with the first and last 2-h periods being statistically significantly different from the three periods in between.

Time-activity budgets

The daytime was spent on two main activities, feeding and roosting, with a small fraction of the time (average of 10% for 25 species) spent on comfort activities (Table 3). Most species spent at least two-thirds of the daytime foraging (Table 3). Species which spent the greatest proportion of the daytime foraging (over 75%) were Wood Sandpiper, Kittlitz's Plover, Common Sandpiper, Turnstone, Ringed Plover and White-fronted Plover, all belonging to guild 2 (the visual surface foragers) and feeding on small prey. Species which spent the least proportion of the daytime foraging (less than 40%) included the larger members of different guilds, such as Grey Plover, Curlew, Black-tailed Godwit, Greenshank, Avocet, Grey Heron and White Pelican. The proportion of time spent foraging seems related to the size of the bird and its guild (Fig. 10). Species feeding on small prey spent a lot more of the daytime feeding (average 66%) than did the fish-eating species (37%), and predominantly socially foraging species spent far less of the daytime foraging (mean of 35% as compared with 63% in the nonsocial foragers). An analysis of covariance, with the arcsin-transformed percentages foraging for each species (Table 3) as the dependent variable, guild as a factor and log body mass as a covariate, yielded a covariance model that explained 60% of the variation in percentages foraging (note that the effect of an interaction between the two independent variables was insignificant). The effects of guild and body mass were both statistically significant ($P < 0.05$) and contributed equally to the explained variance.

DISCUSSION

Diurnal patterns

Waterbird species in the nonbreeding season spent their day feeding, roosting and maintaining themselves with comfort activities and spent a small fraction of time on aggressive behaviour, predator avoidance and commuting between a roost and feeding areas (Myers 1984, McNeil *et al.* 1992). Foraging usually took most of the time. In the coastal lagoons in Ghana, we observed a range of temporal patterns in foraging activity: uniform foraging throughout the day, an early morning and a late afternoon peak, a crepuscular pattern (in pelicans only) and night feeding. Fasola and Canova (1993) contrasted their finding of Grey Herons foraging mainly at night at Lake Turkana in Kenya with the diurnal feeding described by Brown *et al.* (1982). We observed Grey Herons foraging throughout the daylight period and at night, with a peak occurring at midday. At Lake Turkana, Avocets fed throughout the 24 h period (Fasola & Canova 1993), contrasting with a probable predominance

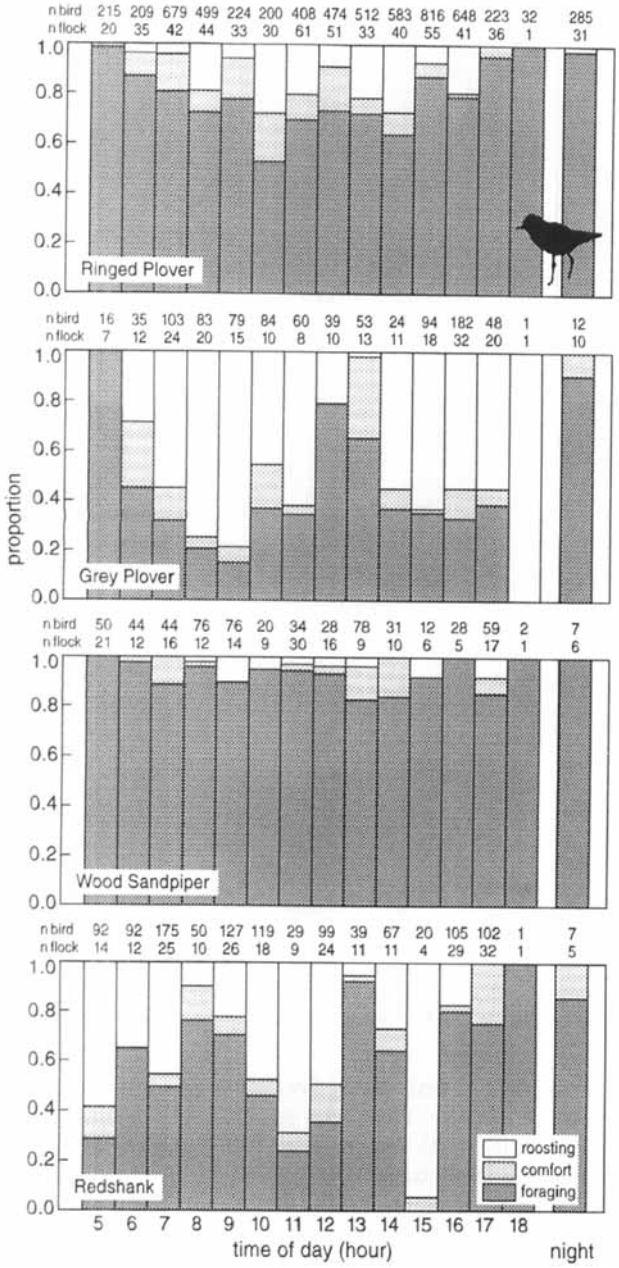

Figure 6. Time-activity budgets of visual surface foraging waders (guild 2) in Songor and Keta Lagoons in October–November 1994. Foraging is indicated by dark shading, comfort behaviour by light shading and roosting by open parts in the histograms. The time budgets are based on the counts of individual birds, but the *n* values for both the number of birds and the number of flocks recorded are given.

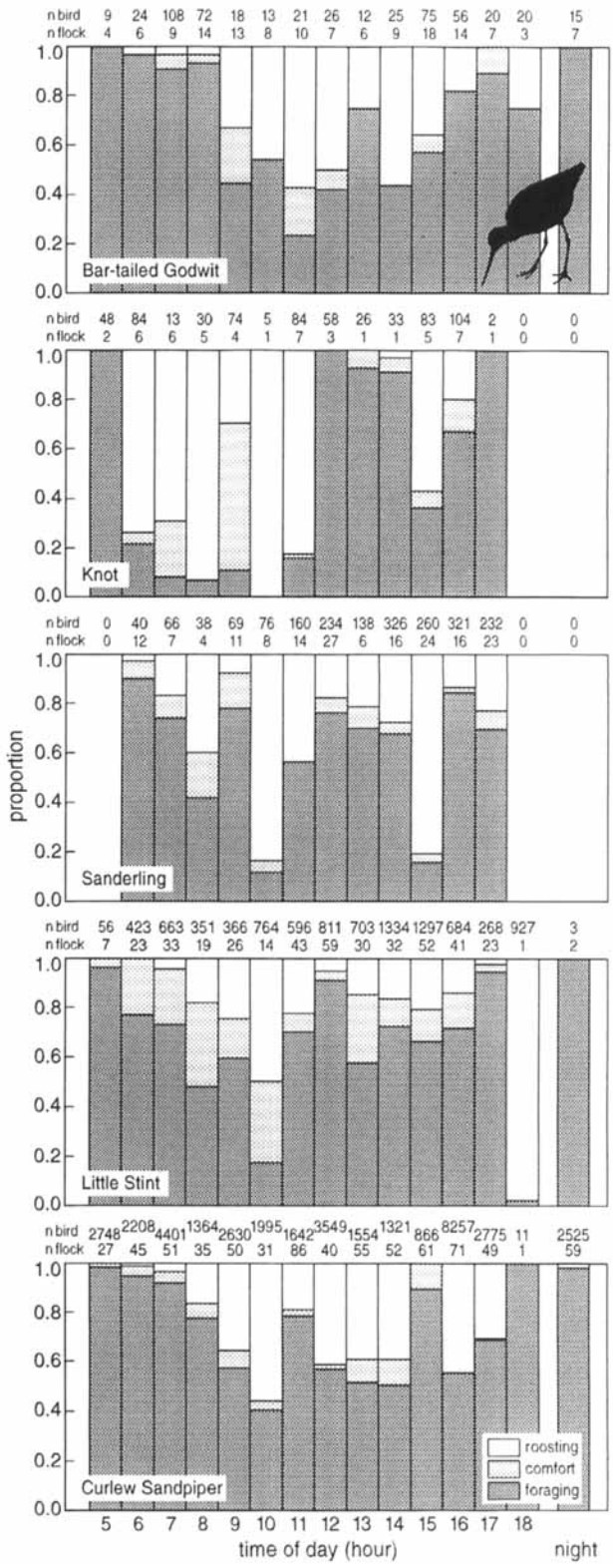

Figure 7. Time-activity budgets of tactile surface foraging waders (guild 3) in Songor and Keta Lagoons in October–November 1994. Presentation as in Figure 6.

of night feeding in the Ghanaian lagoons. Both observations are at variance with the findings in a Senegalese nontidal lagoon, where Avocets fed only in daylight (Zwarts *et al.* 1990).

Such remarkable contrasts in diurnal rhythmicity occur in other waterbird species as well. During their northward migration in Patagonia, southern Brazil and Delaware Bay,

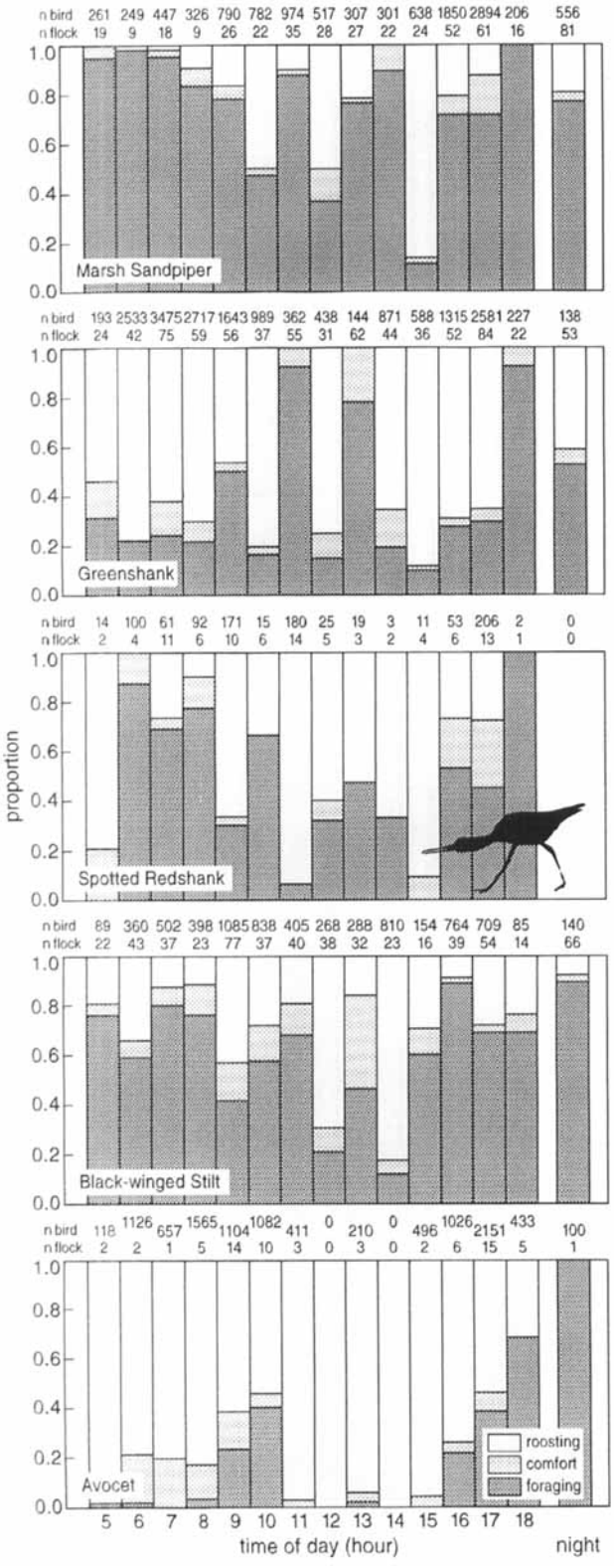

Figure 8. Time-activity budgets of pelagic foraging waders (guild 4) in Songor and Keta Lagoons in October–November 1994. Presentation as in Figure 6.

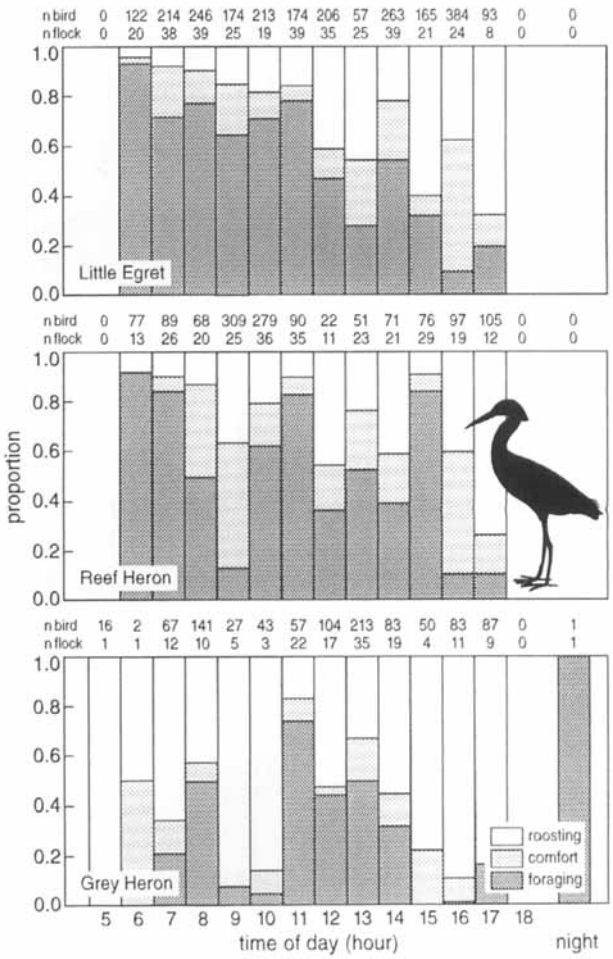

Figure 9. Time budgets of stalking herons (guild 5) in Songor and Keta Lagoons in October–November 1994. Presentation as in Figure 6.

Knots appear to feed only by day (Harrington 1996). In West Africa and Europe, the species routinely feed day and night (Zwarts *et al.* 1990, Piersma *et al.* 1994), and the same happens at stopover sites in New England during the southward migration (Harrington 1996). Burger and Gochfeld (1991) found that the time spent foraging by Sanderlings at beaches in Florida and their diel feeding patterns were significantly influenced by the presence of people within 100 m of foraging Sanderlings. Sanderlings foraged throughout the day on the Ghana lagoons, but at another site, a sandy beach in western Ghana, they showed clear early morning and dusk foraging peaks which were also influenced by tides (Y. Ntiamoa-Baidu, unpubl. data). It follows that the observed patterns in the use of the 24-h day by waterbirds for foraging are not species specific but that the patterns adopted vary depending on the details of the local ecological conditions. This is an area where more research is needed.

Time-activity budgets

Comfort activities comprised the behavioural category that was recorded least often. For the 25 species studied in the

Table 3. *Proportion of time spent on the three different activity categories by waterbirds in Songor and Keta Lagoons in October–November 1994*

Species	Guild[a]	Time spent (%)			Number studied	
		Foraging	Roosting	Comfort	Birds	Flocks
Kittlitz's Plover	2	88	9	3	337	72
White-fronted Plover	2	73	22	4	49	31
Ringed Plover	2	78	13	9	5722	522
Grey Plover	2	37	52	10	901	201
Common Sandpiper	2	84	9	7	58	54
Turnstone	2	84	5	11	64	34
Wood Sandpiper	2	91	4	5	582	178
Redshank	2	53	39	8	1203	226
Black-tailed Godwit	3	20	73	7	2373	11
Bar-tailed Godwit	3	74	21	5	483	126
Curlew	3	31	37	31	548	55
Knot	3	47	41	12	644	49
Sanderling	3	63	32	5	1960	168
Little Stint	3	66	17	16	8334	403
Curlew Sandpiper	3	67	29	4	35,674	654
Marsh Sandpiper	4	68	24	8	10,880	368
Greenshank	4	25	67	8	19,339	679
Spotted Redshank	4	44	45	11	952	87
Avocet	4	20	70	10	10,379	68
Black-winged Stilt	4	56	34	10	6745	495
Little Egret	5	53	27	21	2312	332
Reef Heron	5	46	28	25	1334	270
Great White Heron	5	69	20	10	59	24
Grey Heron	5	33	57	10	973	149
White Pelican	6	23	75	2	1052	5

[a] Guild numbers as in Table 2.

Ghanaian lagoons, an average of 10% (range 2–31%) of the birds observed during daytime were engaged in comfort activities such as stretching, preening or bathing (Table 3). This value is similar to the average of 9% (range 0.3–25%) daytime maintenance activities reported for over 62 bird species from a comparative literature survey (Cotgreave & Clayton 1994).

Fasola and Canova (1993) found that the proportion of time spent feeding by 42 species of waterbirds at Lake Turkana was negatively related to body mass and the size of individual food items and positively to the extent of long distance migration. In Ghana, the proportion of the daytime spent foraging varied between the different waterbird species and ranged from 20% in the Black-tailed Godwit to over 90% in the Wood Sandpiper. Confirming the pattern for Lake Turkana, bigger species and species that fed on larger prey items spent less time foraging (Fig. 10). Studies of a wide range of bird taxa have previously reported that foraging time is inversely related to body size (woodland passerines: Gibb 1954; seabirds: Pearson 1968; coastal waders: Engelmoer *et al.* 1984, Zwarts *et al.* 1990). This general pattern has been attributed to the energetic consequences of body size (Calder 1984), i.e. bigger species need proportionally less food. If intake rate is proportional to body mass (M), as found for coastal waders by Zwarts *et al.* (1990), then foraging time should allometrically scale with $M^{-0.25}$. Zwarts *et al.* (1990) found an exponent of -0.22 for coastal waders wintering in West Africa. For the 25 waterbird species listed in Table 3, a regression of the logarithm of diurnal foraging time (foraging percentage × 13 daylight h) on log body mass yielded an exponent of -0.20 (s.e. ± 0.06, $r^2_{25} = 0.36$), a value not significantly different from -0.25. This supports the interpretation that it is the relative decrease in energy expenditure with increases in body size (on the premise that intake rate increases proportionally with body size) that explains a decrease in the amount of time necessary for foraging.

The analysis of covariance showed that the proportion of time spent foraging by the waterbirds using the Ghana lagoons was related not only to body mass but also to the guild. Predominantly socially foraging species (guild 4; Fig. 10) spent far less of the daytime foraging (mean = 35%) than nonsocial foragers (mean = 63%). We propose, but are unable to evaluate at this point in time, two hypotheses for this. The first is that social foraging may be so profitable that individuals using that style of feeding need to spend

Table 4. *Analyses of variance to determine whether diurnal variations in foraging activity were greater than expected by chance for species of which at least 80 flocks were scanned. The period of dawn, dusk and full daylight (between 4.30 and 18.30 h) was divided into five periods of respectively one 2-hr and four 3-h periods rather than the hourly periods in Figures 6–9. We tested whether the variation between periods was larger than the variation within periods. The bold print denotes species for which the figures were significant at the 1% level. Foraging percentages were based on flock means, normalized by arcsin-transformations*

Species	Number of flocks	R^2 (%)	*F*-ratio
Ringed Plover	**522**	**5.3**	**7.23**
Grey Plover	201	3.8	1.96
Wood Sandpiper	178	2.7	1.21
Redshank	226	3.8	2.16
Bar-tailed Godwit	126	5.2	1.64
Sanderling	**168**	**7.0**	**4.11**
Little Stint	**403**	**3.3**	**3.36**
Curlew Sandpiper	**654**	**2.9**	**4.85**
Marsh Sandpiper	368	2.3	2.09
Greenshank	679	1.3	2.22
Spotted Redshank	87	3.4	0.71
Black-winged Stilt	**491**	**3.2**	**4.01**
Little Egret	332	0.8	0.83
Reef Heron	270	2.5	2.27
Grey Heron	149	4.5	1.69

little time to fulfill their energy requirements. The second is that foraging at night is so profitable that the daytime can be spent at leisure.

Nocturnal foraging

A few waterbird species are known to feed exclusively at night (McNeil *et al.* 1992), but many species are known to feed both day and night in both temperate (Goss-Custard 1969, Heppleston 1971, Pienkowski 1981, 1982, Puttick 1984) and tropical areas (Robert & McNeil 1989, Robert *et al.* 1989, Zwarts & Dirksen 1990, Zwarts *et al.* 1990, Morrier & McNeil 1991, Kalejta 1992, Fasola & Canova 1993, Thibault & McNeil 1994, Rohweder & Baverstock 1996). In temperate areas, where studies on nocturnal foraging were initially concentrated, short day lengths and low air temperatures were used to "explain" nocturnal foraging. Birds would feed at night to compensate for the energy deficit caused by higher energy demands of cold weather and the short time available for foraging during winter (Goss-Custard 1969, Heppleston 1971, Pienkowski 1981, 1982). In the tropics, where temperatures are high and the daylight period is longer, nocturnal foraging has been explained as a means to counterbalance an energy deficit caused by the relatively high demands of activities such as moulting and fat deposition in preparation for migration (Puttick 1979, Morrier & McNeil 1991). Nighttime foraging has also been attributed to its greater profitability in terms of prey availability and accessibility (Dugan 1981, Zwarts *et al.* 1990), and as a means of avoiding predators, kleptoparasitism and human disturbance. Consequently, two main hypotheses have been put forward to explain nocturnal foraging in birds. The "supplementary hypothesis" maintains that nocturnal foraging occurs when daytime feeding has been inadequate to meet the birds' energetic needs, while the "preference hypothesis" proposes that birds prefer to feed at night because it provides the most profitable or safest feeding opportunities (McNeil *et al.* 1992). Both hypotheses imply that diurnal feeding is the norm and that night feeding occurs only as a result of various abiotic and biotic pressures.

Nocturnal foraging has also been linked with the sensory mechanism for prey detection. Two basic sensory mechanisms for prey detection have been described for shorebirds (Robert & McNeil 1989, Piersma 1996a,b): visual, as in plovers, and tactile, as in many sandpipers. The proposition from this is that wader species that feed by touch should be relatively unaffected by darkness (Dugan 1981, Pienkowski 1981, Robert & McNeil 1989, Robert *et al.* 1989), and one would expect, therefore, that birds that foraged at night

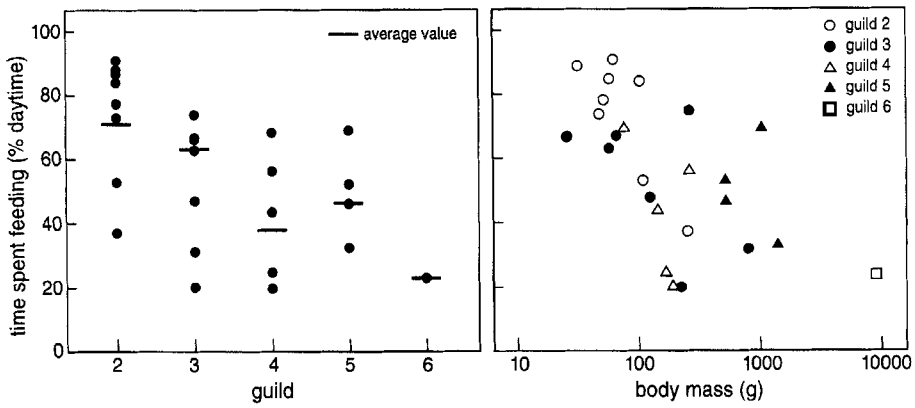

Figure 10. Waterbird species averages of the time spent feeding during daylight in Songor and Keta Lagoons in October–November 1994 as a function of (A) guild and (B) body mass.

would largely be tactile foragers. This proposition is buttressed by the results of an analysis of the sensory bases of nocturnal foraging by Martin (1991), which showed that hearing, smell, mechanoreception and taste were the principal senses used in the detection of food items by birds at night and that vision played only a secondary role. In their study in a tropical lagoon in Venezuela, Robert *et al.* (1989) observed nocturnal foraging in both species that fed predominantly by touch and those that either foraged visually or by both sight and touch. On the basis of the fact that the foraging activities of both visual and tactile waterbirds were influenced by tidal conditions and both fed regularly in darkness, they concluded that nocturnal foraging constituted a natural habit in response to regular limited feeding space and time mainly induced by tides. Fasola and Canova (1993), working on Lake Turkana in Kenya, a static water body, also observed night feeding by both visual- and tactile-foraging species

We observed night feeding in all of the species in guild 4, the pelagic foraging species which used a combination of visual and tactile clues for prey detection, in three species of guild 3, the tactile surface foragers, and in purely visual foragers belonging to guild 5 (Grey Heron) and guild 2 (Ringed Plover, Grey Plover and Redshank). Nocturnal foraging was not related to prey type because both fish and invertebrate eaters were observed to feed at night. Night feeding, therefore, was common in most of the waterbird guilds that used the nontidal lagoons in Ghana. Therefore, nocturnal foraging is a perfectly normal and regular foraging strategy of waterbirds irrespective of the sensory mechanism used to detect prey or the abiotic and biotic conditions prevailing on the feeding grounds.

Water depth selection and management of the lagoons

The choice of feeding habitats varied within and between the guilds and was mainly dependent on two factors: (1) the size of the bird (more specifically, the leg length and height above the ground) and (2) food availability. Water depth is considered to be a key environmental factor controlling the availability of food for the birds in the Ghanaian lagoons. Changes in the lagoon water depth which result directly from rainfall (leading to increases) and evapotranspiration (leading to decreasing depth) influence the salinity and temperature, which in turn affect survival of the prey organisms living in the lagoon. All ground-feeding waterbird guilds, representing the majority of waterbirds feeding in the lagoons, require very shallow water (no deeper than 20 cm). At the high water levels brought about by freshwater input from the catchment, many of the food resources present in the lagoons are no longer available. The length of time for which the water has been at the right depth is also relevant. Thus, the deeper areas of the lagoon and recently flooded areas devoid of prey items were not used by the birds. As the water receded, both fish and invertebrate prey became available for the birds. Surface-foraging waders such as Sanderling and Ringed Plover could obtain their prey only when the water depth was very low and the mudflats were exposed, as happened at the edges of the lagoon. When the lagoons dried up, as large sections did in the dry season, the fish, invertebrates and seeds stranded on the surface of the drying mud could be used for some time by surface foraging waders, but this is likely to be for only a short period. Periodic inundation and drying of large areas of the water body is a regular seasonal feature of both Songor and Keta Lagoons. Neither condition appears to favour the waterbirds. The maintenance of various water depths in different sections of the lagoon system, therefore, is a critical management issue that must be addressed in order to maintain or enhance the value of the Ghana coastal wetlands as waterbird habitat.

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